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FORAGING BEHAVIOR OF EASTERN GRAY SQUIRRELS
ON THE UNIVERSITY OF MAINE CAMPUS

by

Aimee Young

A Thesis Submitted in Partial Fulfillment
of the Requirements for a Degree with Honors
(Zoology)

The Honors College

University of Maine

May 2013

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Abstract

The goal of this study was to observe the foraging behavior of Eastern Gray Squirrels (*Sciurus carolinensis*) on the University of Maine campus. The study tested whether squirrels in a more urban setting followed the optimal foraging theory, or if rarity of a food type played a greater factor in food selection. The study also examined whether urban squirrel behavior mimicked that of wild squirrels when presented with a food type uncommon on campus, but common in other parts of Maine, specifically the acorns of the white oak tree (*Quercus alba*). In three different areas on the campus, squirrels were given a number of different food types: English walnuts (*Juglans regia*), Spanish peanuts (*Arachis hypogaea*), red oak acorns (*Quercus rubra*), white oak acorns, and sunflower seeds (*Helianthus annuus*). Data were collected on which food item was taken and if they chose to eat or cache the item they had chosen. An overall pattern of the order in which the squirrels took the food was then established. Nutritional content was then taken into consideration to see if the squirrels followed the optimal foraging theory and if their behavior correlated with wild squirrels. A chi-square test confirmed the significance of their behavior. It was found that in the face of novel food types, squirrels do indeed follow the optimal foraging theory, and are able to estimate the profitability of food items. They do indeed follow the natural behaviors of eastern gray squirrels found in less urban settings.

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Introduction

Eastern gray squirrels (*Sciurus carolinensis*) are very common tree dwelling mammals found all across the eastern half of North America. Squirrels have distinct dentition with powerful ever-growing incisors and a diastema where typical omnivores and carnivores have canine teeth. They also have sets of premolars and molars for grinding their food (Gurnell 1987). Although their dental structure may be better suited to gnawing or grinding rough vegetations, eastern gray squirrels are omnivores, consuming many different foods from fruits and nuts, to gnawing on bones and eating small birds and reptiles (Thorington & Ferrell 2006). Their natural diets change from season to season depending on what is most plentiful. The autumn and winter diets are mainly composed of seeds and fruits (Gurnell 1987).

It is known that during autumn, squirrels often cache their food items while food is plentiful, and in contrast, search for their cached items and consume them during the winter. They must cache hundreds of food items during the fall since they are active all throughout the year and do not hibernate during the winter. Gray squirrels cache their food in a method called scatterhoarding. Squirrels will cache each individual item in its own shallow hole in the ground, often relatively near the place where the food item was found. They then rely on memory and a keen sense of smell to relocate the food during the winter and following seasons (Gurnell 1987). This method seems to have its advantageous and disadvantageous aspects as food cached by other squirrels who have stored their food in the same area are often found, dug up, and consumed instead. Food is buried in a number of different locations by one squirrel, so defending the food items becomes impossible. As food becomes scarce during the winter months, food is

inadvertently shared communally with other squirrels. Since they must compete against one another for food, the optimal foraging theory should be exhibited by all eastern gray squirrels. The optimal foraging theory states that animals will always choose food items that are most energetically favorable to them based on the nutritional content, minus the energy it takes to obtain and consume the item.

Research has also been conducted on the foraging behavior of eastern gray squirrels in response to acorns of red (*Quercus rubra*) and white oak trees (*Quercus alba*). It is noted by Fox (1982) that squirrels have different responses when presented with the two different types of acorns. Squirrels tend to cache the red oak and eat the white oak acorns. Although there is still some debate between researchers, and preference between the two acorns seems to vary between squirrel populations, most researchers have concluded that the squirrels are able to differentiate between the two and that their differing responses are due to the tannin content of each species of acorn. Red oak acorns contain more tannin than the white oak acorns, and the extra tannin in red oak acorns makes them more bitter tasting. It is believed that squirrels cache the red oak acorns to allow the tannin content to dissipate over time, making the red oak acorns more palatable, while white oak acorns contain less tannin and can be consumed right away (Fox 1982). Studies have also shown that white oak acorns germinate faster than red oak acorns. If they germinate, the squirrels can no longer eat them, as the energy stored in the acorn would then have been lost to the seedling's growth. In response, squirrels are less likely to cache the white oak acorns in the ground unless the embryo of the acorn is removed prior to caching, thereby halting the germination process (Steele 2001). Many studies have been completed about foraging for food items, such as the red and white oak

acorns in natural settings. However, the foraging behavior of squirrels in urban areas, with a plethora of uncommon food types that would not normally be found in the wild, seems relatively undocumented.

Through this study, the hope is to observe urban squirrel behavior when they encounter foods commonly found in natural squirrel habitats, but largely absent in urban settings such as the University of Maine campus, and whether rarity of food types play a greater role than the optimal foraging theory in urban settings. It is hypothesized that urban squirrels will instinctively mimic the foraging behavior of squirrels in locations largely undisturbed by humans, and when presented with rare and common foods, they will be able to forage optimally and choose the food item they will benefit from the most.

Study Sites

Data were collected from three different study sites around campus where squirrels seemed to be most plentiful (Figure 1). These three study sites were picked from a number of sites pin-pointed by Michael Clay (Clay 2006). These sites were spaced far apart, which ensured that the individual squirrels being tested were from different populations. The areas chosen were near a single red oak tree or stand of red oak trees that were producing mast crops of acorns during the fall when the study began. The site labeled “Mainebound” (M on the map provided), was located just south of the Mainebound Adventure Center and Climbing Wall. The second site labeled “Penobscot” (P) was located just northwest of Carnegie Hall. The third site labeled “KnoxAndro” (K) is contained south of the Knox Parking Lot.

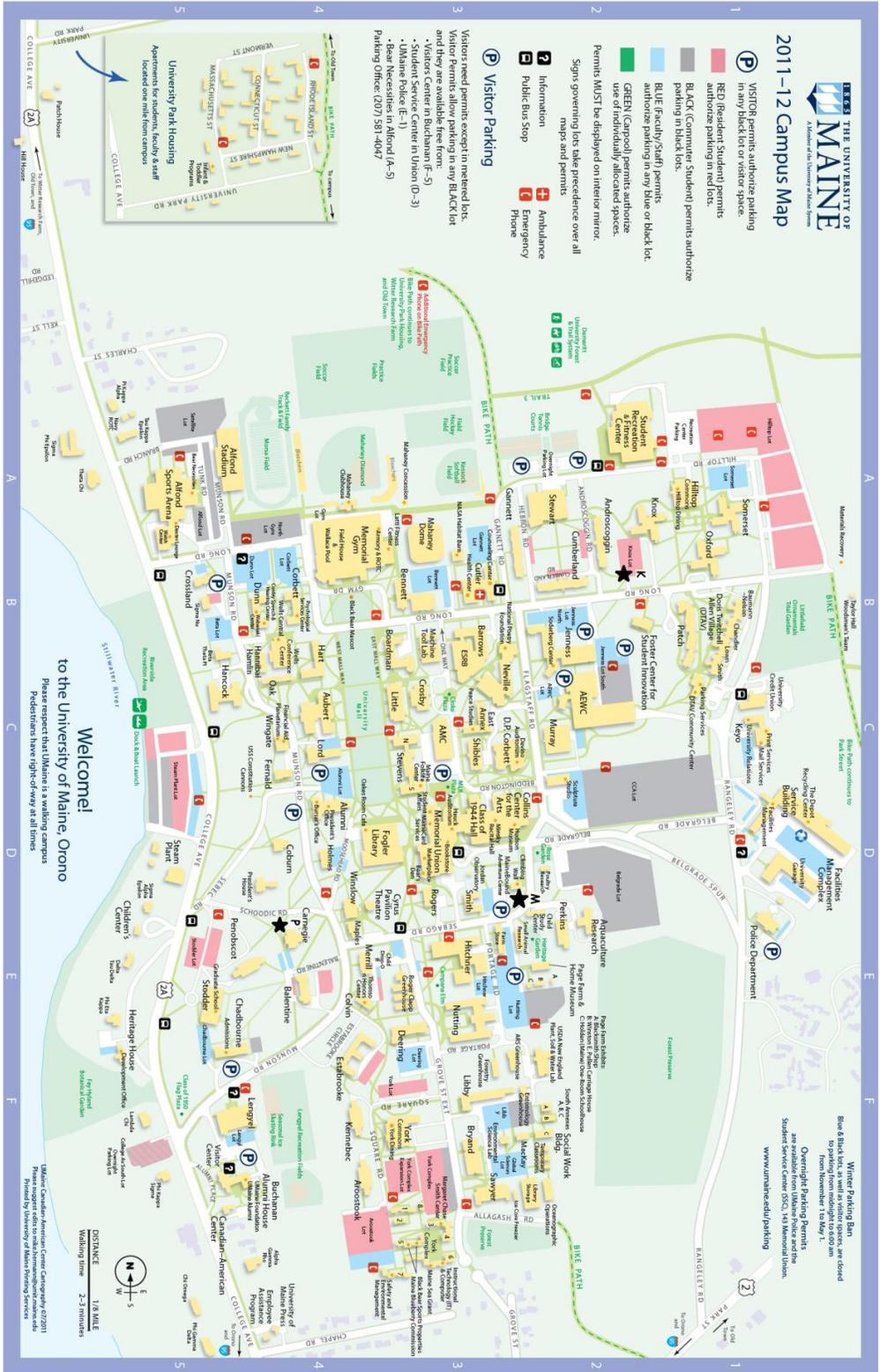


Figure 1. Campus map of the study sites used. Sites are marked with a black star and initials corresponding to each site. M = Mainebound, P = Penobscot, and K = KnoxAndro.

Materials and Methods

Each study site was set up as shown in Figure 2. To avoid confusion and to ensure that existing food in the area did not interfere with the food laid out in the study, a circle about five meters in diameter was swept and cleared with a rake near the base of the tree where squirrels were previously observed to be most active. Red oak trees were used in the fall, while the bases of pine trees in the same area were often used in the winter season where squirrels were nesting. The food was laid out in separate piles to make it easier to identify by sight, but were only about an inch apart, so as to allow squirrels the opportunity to go amongst the piles and choose the food they wanted to take to cache or feed on. The food piles were made to be about the same size with twenty English walnuts (*Juglans regia*), forty unsalted roasted Spanish peanuts (*Arachis hypogaea*), forty red oak acorns, forty white oak acorns, and eighty unsalted and roasted sunflower seeds (*Helianthus annuus*). This was done to ensure that initial pile size was not a factor in squirrel food selection. Excess salt is known to adversely affect squirrels, and raw peanuts are known to contain a toxic mold reported to inhibit an enzyme in the squirrel's body, which is documented to cause fur loss and starvation in squirrels. A lot of salt is also unhealthy for squirrels. So as not to harm the squirrels, unsalted roasted peanuts and sunflower seeds were used. The white oak acorns that were purchased online were shipped from Vermont and had to be disinfected for acorn weevils (*Curculio nucum*) that were found in the shipping package. This was done by soaking the acorns in a tub of cold water for twenty-four hours to drown any acorn weevils hiding within the acorns. The water was then drained and the acorns were left on newspaper to dry for another twenty-four hours. Acorns with visible acorn weevil holes in them were disposed

of and were not used as they were probably hollowed out by the larvae and contained little nutrition. Once the food was placed, a tripod with a camera was set up about ten meters away to record the squirrels' behaviors. The observer stood behind the camera and observations were also taken by hand, recorded in a notebook. Data were recorded on what food item was taken, whether it was cached, which was observed when squirrels left the immediate area, or whether it was eaten, with squirrels usually sitting on the ground or perched in a nearby tree in the area to consume the item. Notes were also made if the same squirrel returned to the site and took more than one food item. Observations were sometimes ended once a pile of a certain food type ran out, as data would then be altered as one of the variable food types was gone. However, at other times, elimination studies were performed where observations were made until either all the food was removed or when squirrels lost interest and left the area. An example of the observations taken in one foraging period can be found in Appendix I. The data were then compiled, chi square tests were performed, and conclusions were drawn. About three hundred trials were done each in the fall and the winter seasons, with a few elimination studies performed in each season as well. The data were taken rotating among different sites each day starting in early October and ending in February the following year. During the fall season, squirrels were most active when the sun rose in the morning as well as in the late afternoon around two p.m. In the winter, squirrels were found to be most active around midday from noon to two p.m., or in the early morning towards the end of the winter season. Winter foraging time was dependent on the personal preference of the squirrel as well as the mildness of the winter season during that particular year (Tonkin 2008).

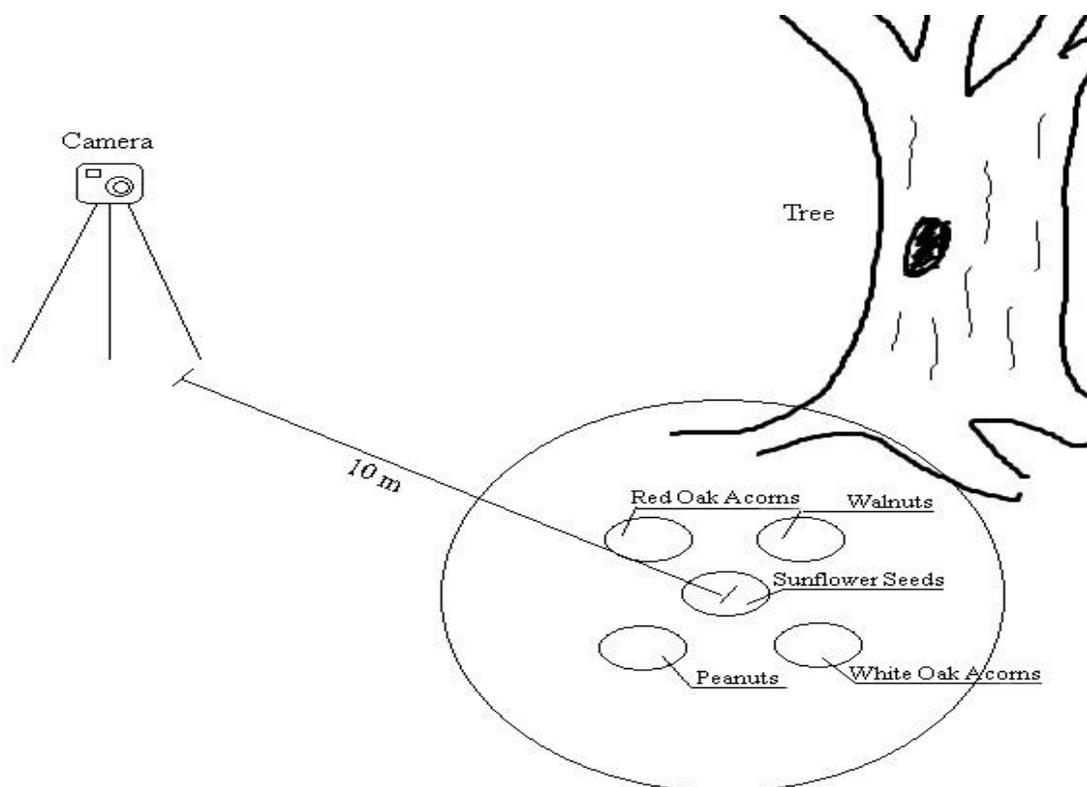


Figure 2. Illustration of a food resource site at the base of a tree. Five piles of food were placed at the base of a tree, each composed of one of the food types offered. A camera was set up with the observer standing behind it to film the squirrels' behavior. Figure is not to scale.

Results

Table 1 lists the different foods used and their nutritional content, which may be a factor influencing squirrel food choice. On the far right side of the table is the estimated daily intake for the recommended amount of nutrients that domesticated squirrels and those in captivity are required to maintain a healthy life. It was based on the information provided from a squirrel vitamin supplement with a suggested serving size of forty grams per day. Values given for domesticated squirrel diets were specified in crude percentages of items such as crude protein, etc, and a serving size. Given the serving size of forty grams, the approximate amount of each item in grams could then be calculated. The

amount of nutrients for walnuts, peanuts, and sunflower seeds was not measured directly, but was taken from the nutritional facts supplied by the distributor of the food product. The nutritional content of red oak and white oak acorns was supplied from tables contained in books by Gurnell (1987) and Steele (2001). Information on certain vitamins or minerals could not be found, and at other times the percentages found in the foods were so small it was insignificant to list in the table, noted by an asterisk. The table shows that although walnuts may have the highest caloric content, they are also missing key minerals and vitamins that the other foods may contain. For example, there is no significant amount of phosphorus in walnuts, but sunflower seeds have the most, although the energy content is very small. Whereas a lot of salt is not good for squirrels, red and white oak acorns contain a small amount that is healthy for a squirrel to ingest. Squirrels must eat a variety of foods to maintain a healthy life, and cannot just feed on the most energy-rich items available.

| | Walnuts (15 g) | Peanuts (1 shelled peanut 2 g) | Red Oak Acorns (3.2 g)¹ | White Oak Acorns (1.4 g)¹ | Sunflower Seeds (0.91 g) | Squirrel Feed (40 g) |
|------------------------------|---------------------------|---|---|---|---|-------------------------------------|
| Crude Protein | 1 g | <0.25 g | -* | -* | 0.027 g | 7.6 g |
| Crude Fat | 4 g | <0.46 g | -* | -* | 0.045 g | 1 g |
| Crude Fiber | 0.4 g | <0.11 g | -* | -* | 0.012 g | 14 g |
| Calcium | 0.12 g | 0 g | 0.062 g ² | 0.038 g ² | 0.002 g | 0.8 g |
| Phosphorus | - | <0.15 g | 0.087 g ² | 0.099 g ² | 0.023 g | 0.32 g |
| Vitamin A | <0.12 g | 0 g | -* | -* | < 0.002 g | 105.822 IU |
| Sodium | 0 g | 0 g | 0.003 g ² | 0.003 g ² | -* | 0.32 g |
| Potassium | 0.08 g | < 0.007 g | 0.923 g ² | 0.918 g ² | 0 g | -* |
| Magnesium | 0.25 g | < 0.15 g | 0.062 g ² | 0.070 g ² | 0.027 g | -* |
| Nitrogen | -* | -* | 1.000 g ² | 1.120 g ² | -* | -* |
| Calories (kcal/g) | 40 | 6 | 5.45 ² | 4.17 ² | 0.576 | -* |

Table 1. Comparison of the different nutrients, minerals, and caloric content contained. Items marked with an asterisk show that the nutrient or mineral was not given, present, or too small to be recorded. 1. Steele (2001). 2. Gurnell (1987)

Each food item was also compared visually to see if size was also a determining factor for food selection. The items were lined up with one another against a scale according to caloric content to see if size correlated with the energy contained in each item. As Figure 3 shows, items such as the white oak acorn are clearly larger than the red oak acorn, yet contain less energy. This allowed size to be ruled out as a contributing factor to food selection, as items with the most caloric content were selected first.

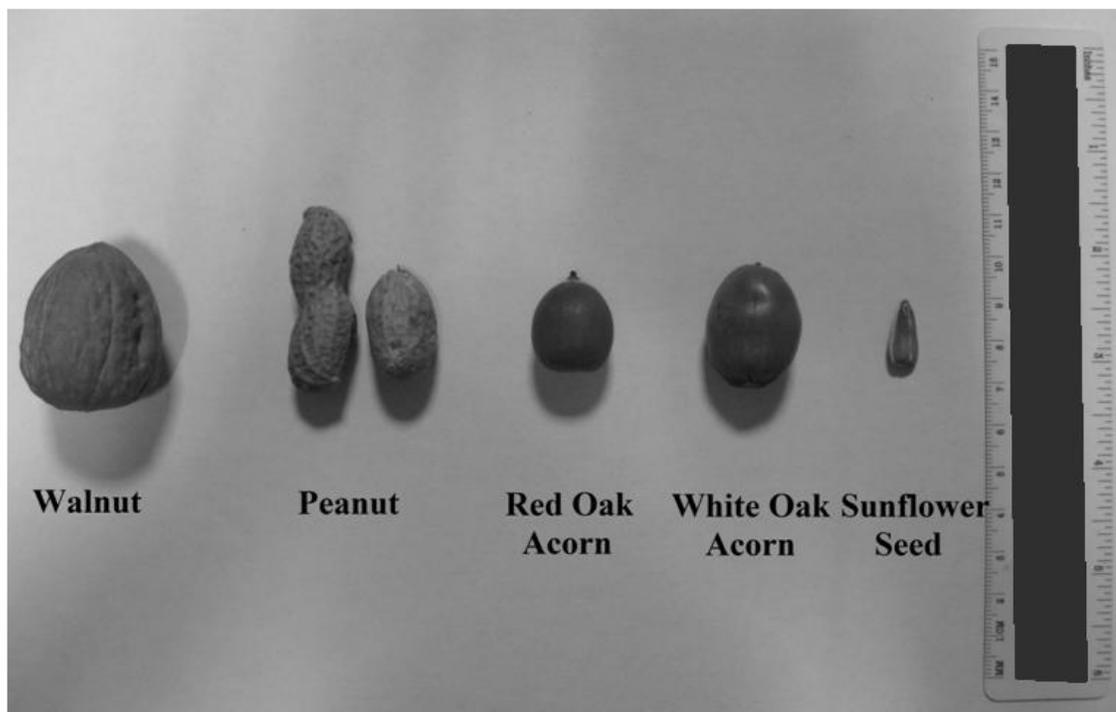


Figure 3. Comparison of each food item according to its size. Items are ordered based on descending caloric content with walnuts containing the most calories and sunflower seeds containing the least.

Data compiled and presented in the following sections are based on observations taken until the pile of one food item was fully depleted, rather than from elimination studies. Since data were successfully collected at all three sites and squirrel behavior remained the same at each location, the data were analyzed as a whole rather than broken down by each site. To compare fall and winter behaviors, data collected during the two

different seasons were separately quantified and displayed (Figures 4 and 5). Percentages were used, rather than the actual total number of each food item that was consumed, since amounts of each food type offered in each pile differed. As mentioned earlier, the original intention of offering different amounts of each food type was to eliminate pile size as a variable in terms of initial squirrel foraging responses. In Figures 4 and 5, food types are ordered according to the caloric content with walnuts having the greatest caloric content per nut, and sunflower seeds having the least amount of energy per seed. In the fall, squirrels removed more walnuts (55.2%), than red oak acorns (24.0%), or peanuts (23.1%), or sunflower seeds (3.33%). White oak acorns were removed the least at a rate of 2.62%. Winter data showed more drastic differences in percentages between all the food types, with walnuts again being the food most likely to be taken at a high rate of 68.9%, with peanuts second at 33.7%, red oak acorns third (22.5%), white oak acorns fourth (2.18%) and sunflower seeds hardly removed from the study sites at all with a removal rate of 0.87%. Rates of removal for white oak acorns, and sunflower seeds were higher in the fall than in the winter while peanuts were taken more often in the winter. Percentages of red oak acorns removed from the sites remained relatively constant. Winter seasonal patterns accurately favored the optimal foraging theory as items with the most caloric content were removed at a greater percentage than items that provided less energy based on caloric content. In the fall, red oak acorns were taken slightly more often than the peanuts. However, the fall data still generally follows the pattern of the higher energy items being removed more often than those food types that contained lesser amounts of energy.

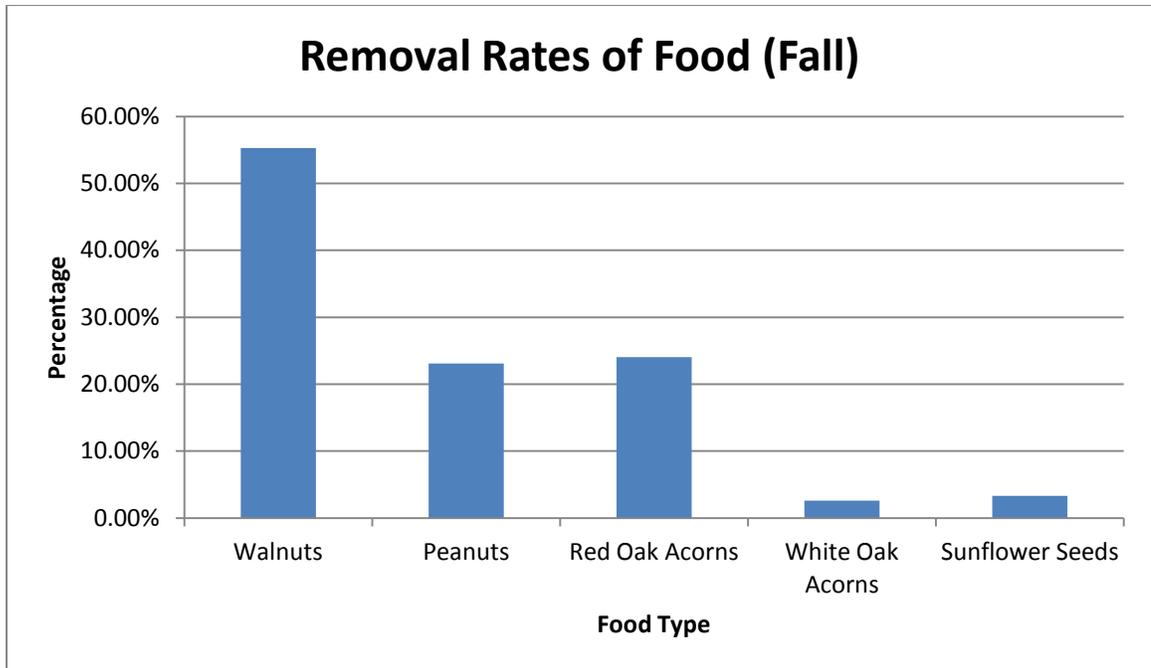


Figure 4. Percentages of each food taken out of the total amount of food that was offered for each type during the fall season.

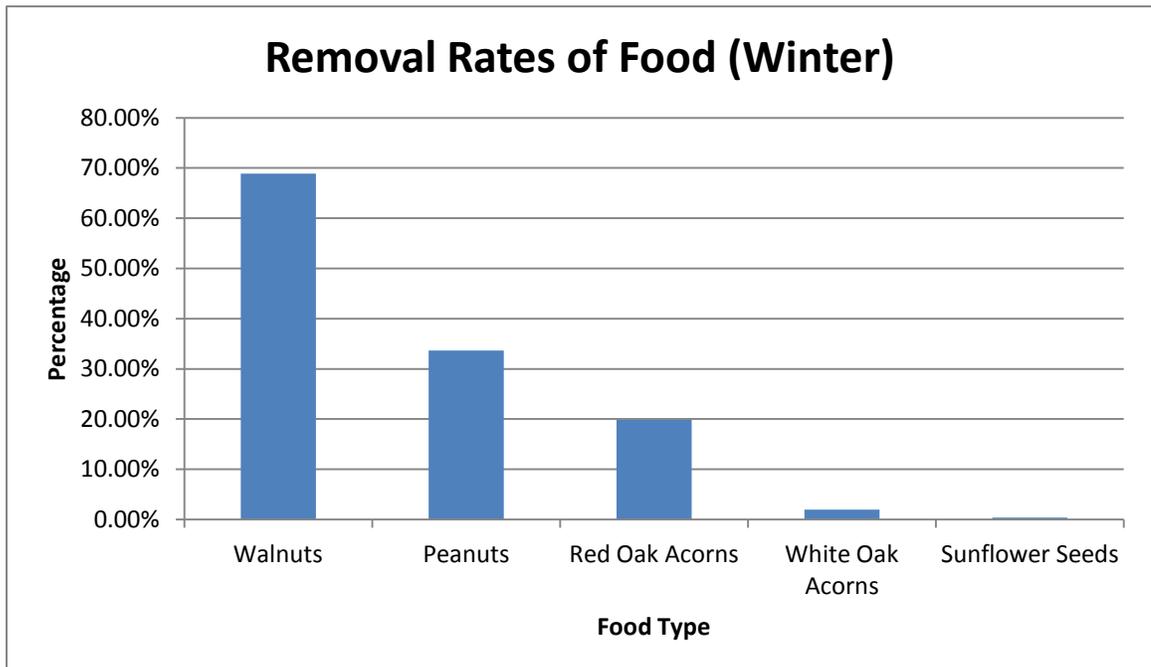


Figure 5. Percentages of each food taken out of the total amount of food that was offered for each type during the winter season.

Figures 6 and 7 illustrate what the eastern gray squirrel’s diet would be if they only fed on the food items offered in the study. The total energy consumed in calories (kcal/g) was calculated based on the caloric values of each food type, which found in Table 1. The calories of each food item were then multiplied by the amount of that food that was taken by the squirrel and displayed in Figures 5 and 6. In both the fall and the winter, walnuts composed the largest portion of their diet at about eighty percent. Peanuts accounted for more of the squirrels’ diets during the winter with thirteen percent, instead of the ten percent in the fall. Red oak acorns composed about the same amount of the fall and winter diets. The energy obtained from white oak acorns and sunflower seeds were so minimal for both seasons that they barely show on the graph.

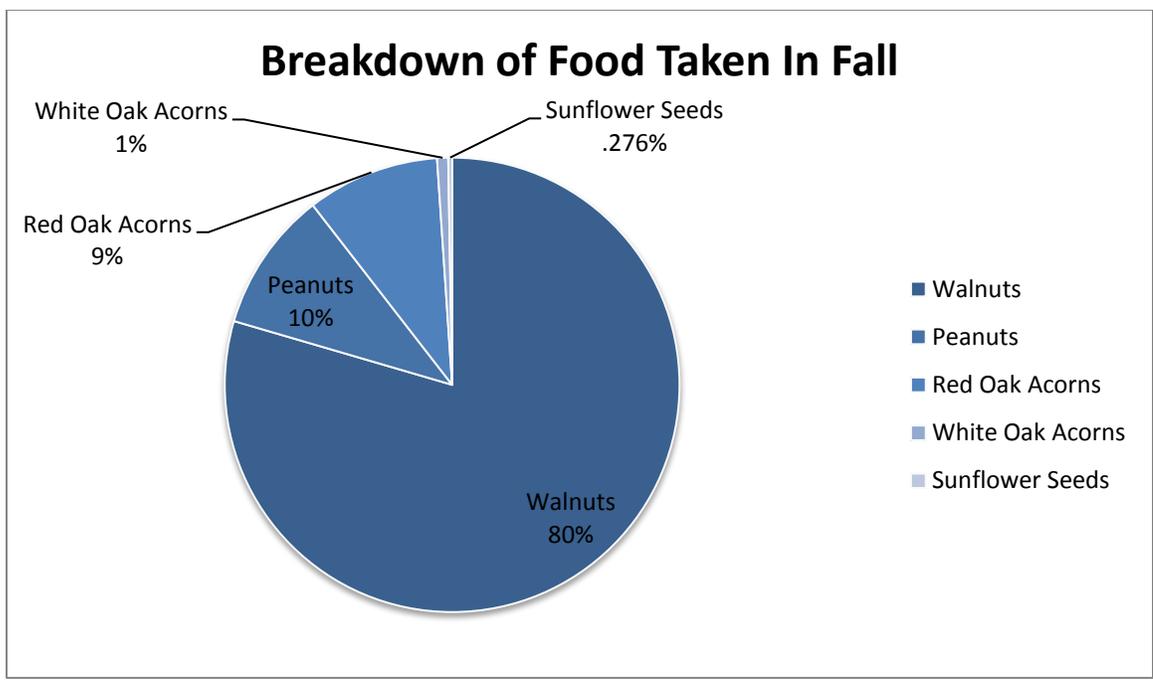


Figure 6. The amount of particular foods taken in relation to each other in terms of caloric content during the fall season.

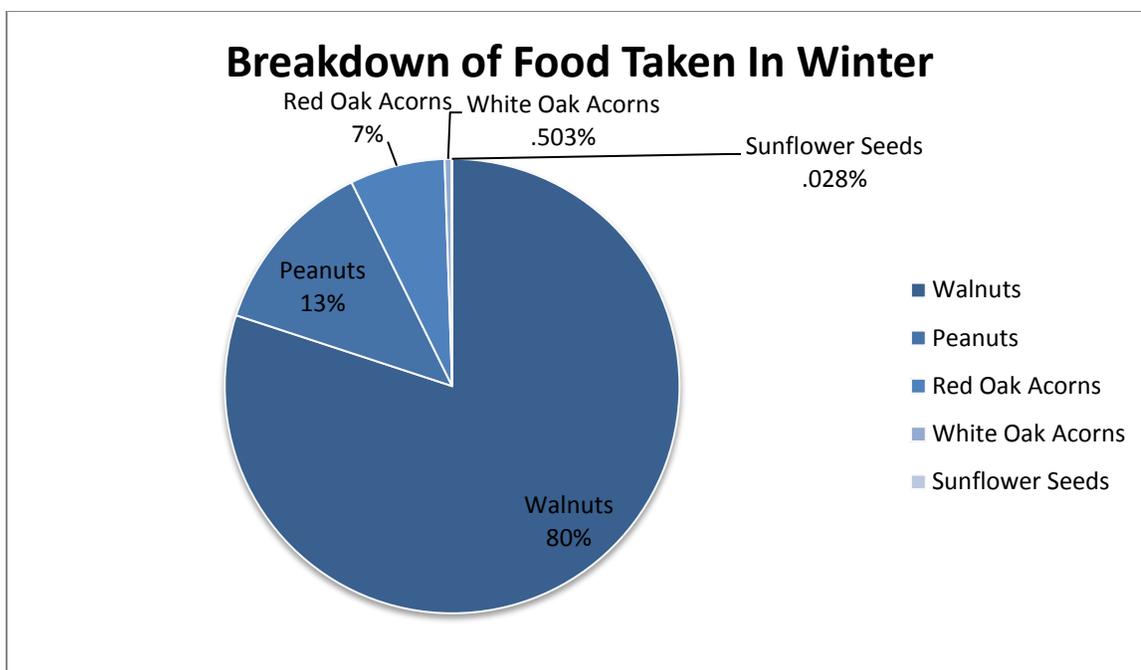


Figure 7. The amount of particular foods taken in relation to each other in terms of caloric content during the winter season.

Although food was taken, it was not always immediately consumed after the squirrels chose a particular food type. This is important to take into account in analyzing the optimal foraging theory. Figures 8 and 9 break down the foods taken even further, separating the percentages of each food type that were cached and consumed. Again the food types are arranged according to caloric content, with walnuts containing the most energy, and sunflower seeds containing the least. In both seasons, it is observed that harder shelled items are cached such as the walnuts and the red oak acorns, while softer shelled items including the white oak acorns, peanuts, and sunflower seeds were more often consumed at the site. During the fall season, many food items were both cached and consumed, while the winter produced more radical results. In the winter, walnuts were only cached, and white oak acorns and sunflower seeds were strictly eaten.

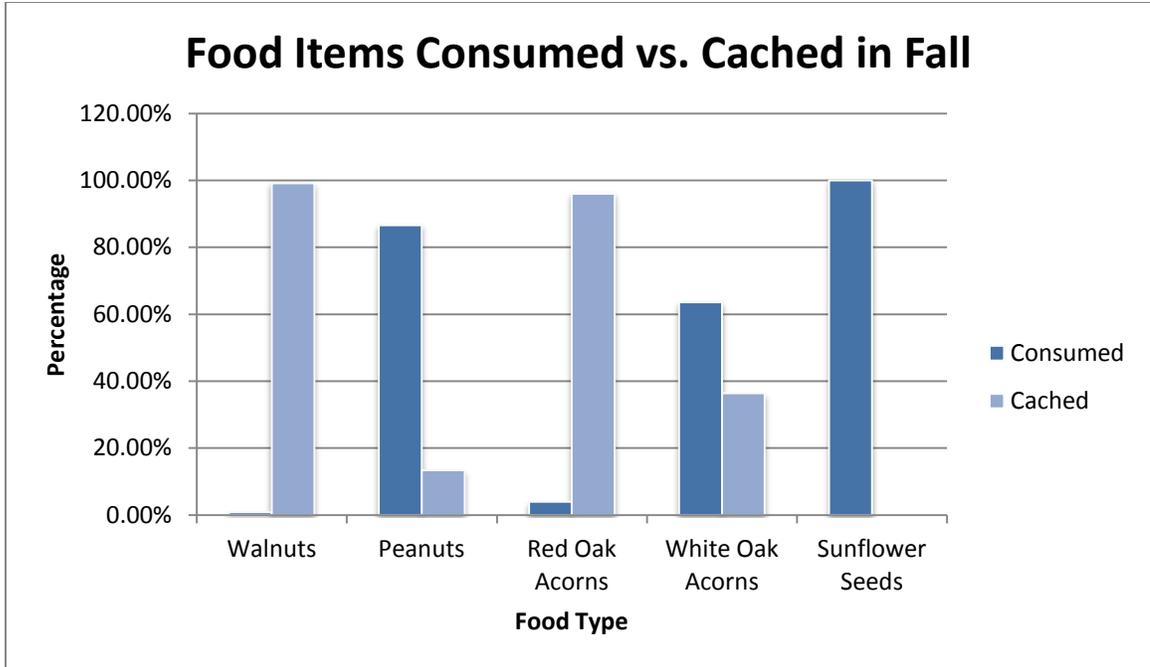


Figure 8. Percentages of food items that were cached or eaten after a squirrel chose the item. Harder shelled foods were cached more often than soft shelled items.

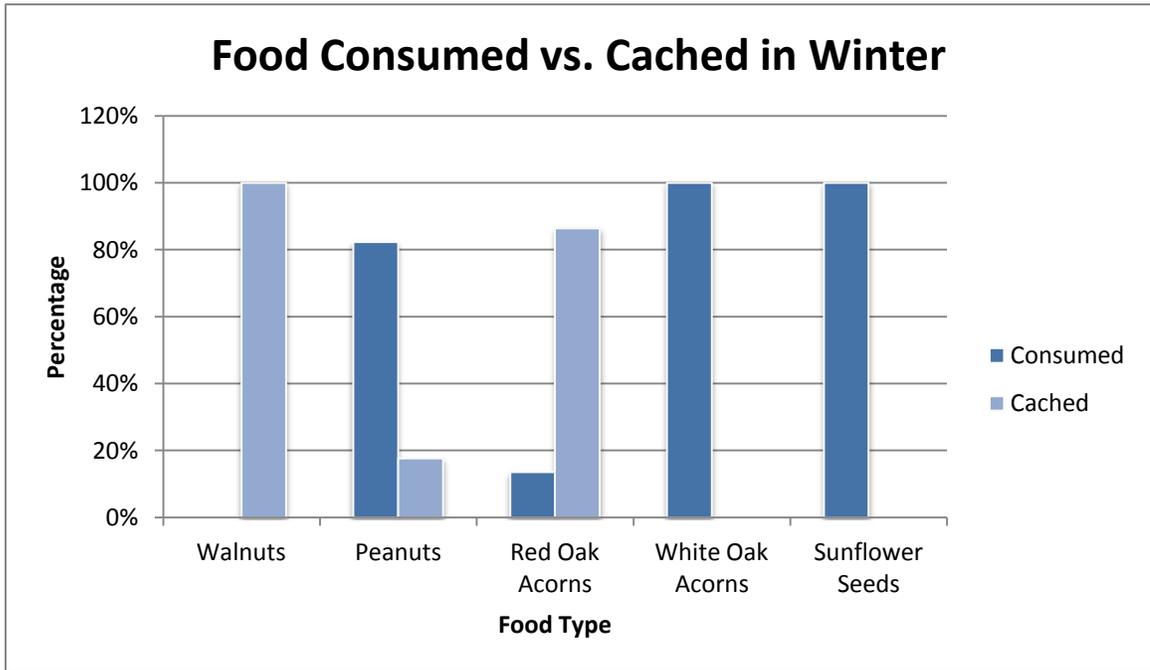


Figure 9. Percentages of food items that were cached or eaten after a squirrel chose the item. Harder shelled foods were cached more often than soft shelled items.

Chi square tests were then completed to further test whether observed behavioral patterns were significant (Table 2). One set of tests examined the observed results, using the values shown in Figures 4 and 5 versus the null hypothesis, that eastern gray squirrels had no preference or did not follow the optimal foraging theory. This would mean that the chances of a food type being taken were equal for all items. The second chi square test analyzed the observed results versus the expected results based on caloric content. The food with the highest caloric content (walnuts) was used as the basis for the expected values of the other food items with walnuts having an expected value of one hundred percent, peanuts having an expected value of fifteen percent as the energy contained in the legume is fifteen percent of that of the walnut, and so on. This would mean that the walnuts are expected to be chosen one hundred percent of the time, because they have the most energy, while peanuts would have a fifteen percent chance of being chosen by the squirrel. If the chi square values are greater than 0.05, the behavior exhibited by the eastern gray squirrels are significant. All values calculated were greater than 0.05 which meant that conclusions can be drawn from the observed behaviors.

| Food Item | Chi Square Value (α) Using Null Hypothesis | Chi Square Value (α) Using Expected Values |
|---------------------------------|---|---|
| Walnuts (f) | 8.269 | 45.078 |
| Peanuts (f) | 2.798 | 10.383 |
| Red Oak Acorns (f) | 3.707 | 16.481 |
| White Oak Acorns (f) | 14.247 | 5.119 |
| Sunflower Seeds (f) | 7.284 | 29.250 |
| Walnuts (w) | 13.195 | 40.647 |
| Peanuts (w) | 16.580 | 35.914 |
| Red Oak Acorns (w) | 0.310 | 5.767 |
| White Oak Acorns (w) | 15.872 | 6.516 |
| Sunflower Seeds (w) | 18.292 | 0.223 |

Table 2. Chi square values. Null hypothesis can be rejected when alpha is greater than 5%. “f” stands for foods taken during the fall, while “w” stands for winter food items.

Discussion

Although the eastern gray squirrels on the University of Maine campus live in a more urban setting and constantly come into contact with the human population that shares the same area, they still exhibit the natural behaviors of those in more natural settings. The data are valid since a number of different individuals and three different populations were studied.

Doebel and McGinnes found that the home range of an individual squirrel is 0.49 ha, the greatest lateral distance being 136.7 m (1974). Each study site was farther apart than this distance, which insured that different populations were being observed. Squirrels regularly visit certain areas of their home range at certain times of the day, often using the same paths or tree branches to get to certain areas, so the study was sure to be sampling from the same three populations of squirrels during each feeding session (Connolly 1979). This territory range allowed the observer to recognize individual squirrels and note which squirrel was taking what food, usually by their tails which were different thicknesses and may have had parts of fur or entire parts of the tail missing. The only time squirrels will travel great distances is when they are released into an unfamiliar area and have not established a territory (Flyger 1960). Since there was no human interference with the squirrels on campus, it was safe to say that the populations remained somewhat constant.

The chi square values show that squirrel preference for more energy-rich items was significant. Since the eastern gray squirrels specifically sought one food before another and usually depleted one food type before moving onto another, the null hypothesis can be rejected. The squirrels had a preference for one food over another so

not all food items had the same chance of being taken. This was also shown in the second set of chi square tests, where the expected values show that squirrels would take all foods, but more energy-rich items at a higher rate. Instead it was observed that squirrels will continually choose the items with the most caloric content, exhausting that source before moving on to lesser items.

Although the squirrels exhibited the optimal foraging theory to some extent, there were some minor differences. During the fall, squirrels more often took red oak acorns rather than peanuts, the latter of which contain more energy, which may be due to their mindset to cache food, rather than consume it since peanuts would not survive in the ground through the winter. They often preferred to feed upon sunflower seeds instead of the white oak acorns, which were only consumed when no other food choices were present if at all as exhibited in the elimination studies. This may be because the white oak acorns had to be soaked in water for twenty-four hours, causing the tannins and possibly other vitamins or minerals to leech out of the acorns into the water. This would make them less profitable to consume as well as possibly make them less palatable for the squirrels. Squirrels would often be seen picking up a white oak acorn and biting into it as if to test what it tasted like. Many times they would put the acorn back down and take another food item. In other studies, squirrels are observed performing the same behavior, as biting a small part of the acorn will also tell the squirrel if an acorn is rotten, in which case they will discard the acorn and find another (Steele 2001). However, in the winter, the eastern gray squirrels followed the optimal foraging theory entirely, although they still neglected to eat a lot of white oak acorns. Since food sources are scarcer during

the winter, perhaps squirrels were more pressured to eat items that had a higher energy content, despite the peculiar taste of the water-soaked white oak acorns.

A similar study conducted in New York looked at the foraging behaviors of eastern gray squirrels in response to foods that were naturally dispersed in a heavily forested area. Lewis (1982) reported that they did follow the optimal foraging theory, the amount of each type of nut consumed being directly proportional to the energy content. However, the squirrels in the study had a preference for hickory nuts even though they provided the least amount of energy. It was concluded that this was because the hickory nuts minimized the risk of predation and other dangers (Lewis 1982). Other factors of the optimal foraging theory such as the energy required to obtain the food item and predatory risk were not present when data was taken since all the food was in a small area and the squirrels were not at risk from predators like birds.

The University of Maine campus, and other more urban areas, provide unique habitats where squirrels are somewhat protected from their natural predators, especially aerial predators like hawks. It was noticed that their predator response tactics are modified in areas with high human traffic, only fleeing when humans approached at shorter distances, while squirrels in low human activity areas fled when humans approached at longer distances (Cooper 2008). Since humans are less likely to hunt squirrels on the university campus than other natural predators, squirrels seem to let their guard down and are more often found scavenging for food, even those more unnatural food types like sunflower seeds. They will forage near human populations, especially risking their lives to feed in areas with less tree cover (Bowers and Breland 1996).

The behavior of eastern gray squirrels in this study did not change in response to the changing seasons. Although it is known that the squirrels may change their foraging times from early sunrise in the spring through the fall, to about midday during the winter and early spring (Bahnak & Kramm 1977), their behaviors exhibited toward food choice and whether to cache or eat the items did not vary greatly. Since eastern gray squirrels are active all throughout the winter, they allow their body temperatures to go through greater change during this season, exhibiting heterothermy (Pereria et al 2002). Even with this adaptation, energy requirements still differ quantitatively during the fall and winter seasons, with the winter requiring greater energy consumption as a result of increased heat loss (Byman et al. 1988). In spite of this, as the study showed, all three squirrel populations continued to forage optimally. They also exhibited the same behavior in response to the two different types of acorns in both the fall and the winter. The squirrels almost always chose to eat the white oak acorns, and most of the time they chose to cache the red oak acorns rather than feed on them. Perhaps the reason why the squirrels sometimes ate the red oak acorns was because they have developed a taste for them and the higher tannin levels do not affect them. The University of Maine campus has a large population of red oak trees scattered throughout the area, while white oak trees are less common, since they are found in the more southern portions of the state.

Although there were many instances of squirrels on campus caching walnuts and red oak acorns in this study, there are no reported instances of eastern gray squirrels caching food items during the winter season. The reason why squirrels may have cached these items during the winter, which they would normally only cache in the fall, is probably due to its abundance at the study site. The squirrels could not eat all of the food

provided and perhaps they realized it is better to store this new found food source before it is gone. It is concluded that squirrels will always want to choose the most energetically favorable food, but that the storability of food also plays a part in what they choose to do once they obtain a certain food item.

The shells of the peanuts, white oak acorns, and the sunflower seeds are very thin and easy to break, while the walnuts and the red oak acorns have thicker shells. The squirrels do roll the acorns around in their paws and bite them tentatively, as if to test the strength and durability of the shells (Steele 2001). The squirrels seem to determine that if cached, the softer shelled items may spoil. The eastern gray squirrels may also assume that the soft-shelled food items may germinate if cached in the ground, as opposed to the harder shelled items which may last longer, instinctually categorizing these rare food items as related to red and white oak acorns.

Caloric content seems to be the overriding factor in eastern gray squirrel foraging activity. Lewis found that squirrels will forage more abundantly in areas that contain a higher energy food though its abundance may be disproportionately low, even if an area abundant with food thought of as preferred is also present (1980). It is actually common for squirrels to refuse different food types if they feel that it is not energetically favorable, or that it does not offer the nutrients they need. Havera and Nixon observed the foraging behaviors of eastern gray squirrels and fox squirrels over two winters that were provided with an abundance of corn. It was found that squirrels did not readily use the food supply because the corn was not a nutritionally adequate food source (1980). Although the walnuts were lacking in or showed minimal amounts of phosphorus, sodium, magnesium, and nitrogen, they were still taken first and the walnuts were often the item that would

end the study for the day, as the walnuts were depleted first. The items that were depleted in the elimination studies were removed depending on their caloric content, with walnuts being removed first, and sunflower seeds or white oak acorns being removed last. The reason white oak acorns were sometimes removed last was probably due to the way they were prepared prior to the study (see pg 6). Although some studies have concluded that size plays a factor, such as in the feeding of fox squirrels (*Sciurus niger*) (Tatina 2007) this does not seem to be the case for eastern gray squirrel as some of the peanuts were smaller than the acorns, but the squirrels still chose to consume them. White oak acorns were larger than the red oak acorns as well as some of the peanuts, but the latter two items were always chosen before white oak acorns.

As a result of the eastern gray squirrel's capacity to estimate the energetic profitability of food items, this may be one of the reasons why they seem to have an easier time adapting to urban settings, and why they are encroaching on other squirrel species' territories. There have been several studies conducted in Britain documenting the decreasing range of the red squirrel (*Sciurus vulgaris*) and growing population of eastern gray squirrels. In Britain, the eastern gray squirrel is an invasive species, taking over red squirrel territory as if there was an absence of competition between the two species (Okubo 1989). Studies in North America also observe territorial exchanges between eastern gray squirrels and fox squirrels (*Sciurus niger*). Both red and fox squirrels feed on similar food items as eastern gray squirrels, so something else must be at play.

Studies have been conducted on the red squirrel and the fox squirrel, showing that their foraging behavior is slightly different than that of eastern gray squirrels. Although

red squirrels are known to also follow the optimal foraging theory like eastern gray squirrels, they have a central cache or a few in which they store their foods instead of scatterhoarding them in holes in the ground. Red squirrels are half the size of eastern gray squirrels so with eastern gray squirrels being larger, they are able to chase red squirrels from their central caches. Individual eastern gray squirrels are also observed having larger territories which overlap with one another and create isolated island-like territories for red squirrels (Reynolds 1985). If the red squirrel loses its cache, it loses much of the food it had stored and may not survive to the next year. Fox squirrels, are observed to scatterhoard their food in the ground as well (Stapanian 1978). However, they have been categorized as opportunists and generalists when it comes to foraging behavior. In the order of food preference, fox squirrels preferred “white oak...acorns, black oak (*Quercus velutina*) acorns, red oak...acorns, walnuts, and corn” (Flyger & Gates 1982). Tatina confirmed this in a study he performed. Fox squirrels, when given items that were energetically equal, but had different costs, chose to eat the items with greater cost, even though they lost more energy due to handling. Fox squirrels also chose to consume items that lessened the time needed to find them, but not necessarily handling time (Tatina 2007).

The changing tree distribution due to the changing climate also favors the survival of eastern gray squirrels. Since gray squirrels did not occupy the hardwood niche in Britain as they usually do in other areas, red squirrels adapted to live in mixed hardwood forests in Britain, as well as the conifer forests where they are normally found. However, climate models in Britain predict that the tree cover will drastically change in the future. While hardwoods are not seen as particularly affected by increasing temperatures,

important conifer species are expected to lose a major portion of their habitat (Haman & Wang 2006). Another study confirmed this, citing specifically that red squirrels that were modeled for the pine woodland habitat were observed to lose considerable climate space (Berry et al. 2002) with other flora replacing the pine woodland habitat. This trend can be traced all throughout the world, with similar changes occurring in North America as well. Since hardwoods are predicted to be less effected, these trees could then spread into areas where pines and conifers once stood. This, along with the larger territory size cited by Lewis (1980) would allow eastern gray squirrels to expand their habitat.

Eastern gray squirrels are also observed to have adapted to more urban areas that often have less tree cover than a forest undisturbed by humans (Cooper 2008). This is supported by a study conducted in St. Louis County, MO which observed an increase in eastern gray squirrel population with increases in food supply by bird feeders in urban and suburban areas where ornamental trees were being planted (Sexton 1990). Although fox squirrels are normally found here, they prefer tall stands of forests adjacent to large open grasslands. With urbanization, trees are felled and buildings and other structures are built, destroying the pure stands of forests and open areas that fox squirrels prefer. With eastern gray squirrels' abilities to continue to recognize the energetic profitability of certain foods, even in an urban setting with little tree cover, along with a growing territory with favorable hardwood trees, they can easily and quickly intrude and take over red and fox squirrel habitat.

Conclusion

Eastern gray squirrels on the University of Maine campus come into contact with many different food types. This study concludes that eastern gray squirrels still follow the optimal foraging theory even when presented with natural foods they have never seen before. They are able to estimate the energy contained in food items and that generally provides the driving force in their foraging decisions. Although their decisions seem to be mostly based on caloric content, some foods do contain vitamins and minerals that others do not, so squirrels may choose to feed on different items as well. Shell thickness and the likelihood that items will still be viable once cached underground also seems to play a factor, especially in terms of foraging behaviors. Items with thicker shells were often cached, while softer shelled food items were consumed on the spot. Eastern gray squirrels on campus react to different food items in similar ways to those squirrels that find some of the same naturally occurring food in less populated areas. Specifically they cached the red oak acorns and chose to eat the white oak acorns. With their ability to adapt to urban settings, and feed on a variety of items, eastern gray squirrels are encroaching on the habitats of other squirrels, endangering the survival of these other species.

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Appendix A:

November 2nd, 2013 3:00 pm at Penobscot (P)

| Squirrel (noted by symbol or lack thereof) | Food Type | Cached (C) or Eaten (E) |
|---|---|--------------------------------|
| | Walnut | C |
| • | Walnut | C |
| • | Walnut (picked up white oak acorn first, then dropped for walnut) | C |
| | Walnut | C |
| • | Walnut | C |
| □ | Red Oak Acorn | C |
| □ | Red Oak Acorn | C |
| • | Walnut | C |
| □ | Walnut | C |
| • | Walnut | C |
| ~ | Peanut | E |
| • | Walnut | C |
| ~ | Peanut | E |
| * | Walnut | C |
| * | Red Oak Acorn | C |
| | Walnut | C |
| * | Walnut | C |
| | Peanut | E |
| • | Walnut | C |
| * | Red Oak Acorn | C |
| | Walnut | C |
| * | Walnut | C |
| • | Walnut | C |
| * | Walnut | C |
| | Peanut | E |
| • | White Oak Acorn | E |
| • | Walnut | C |
| • | Red Oak Acorn | C |
| ~ | Walnut | C |
| ~ | Walnut | C |

Author's Biography

Aimee Young was born in Newton, Massachusetts on April 26, 1991. She grew up in Bedford, Massachusetts, and graduated from Bedford High School in 2009. She is currently majoring in zoology and has a minor in Native American studies. Upon graduation, Aimee will continue to work at a dog kennel in her hometown and hopes to work closely with wild animals in animal management programs or perhaps work towards her masters in the future.